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ORIGINS OF THE AUSTRALIAN SCINCID LIZARDS: A PRELIMINARY REPORT ON THE SKINKS OF RIVERSLEIGH.

MARK N. HUTCHINSON

South Australian Museum,
North Terrace, Adelaide, SA 5000, Australia.

ABSTRACT

The fossil skinks from the Oligo-Miocene to Pliocene limestone deposits at Riversleigh, Queensland, include eight or more taxa representing the *Sphenomorphus, Egernia* and *Eugongylus* Groups of the subfamily Lygosominae. Some of these are practically indistinguishable from living taxa, while others appear to have left no descendants. This is the richest fossil skink fauna yet recorded in Australia and probably the world. The presence in the early Miocene of all three of the major lygosomine lineages present in the modern Australian fauna means that these lineages arose no later than the early Tertiary.

Keywords: Lizards, Scincidae, fossils, Miocene, Australian fauna.

INTRODUCTION

The fossil deposits of the Carl Creek Limestone, Riversleigh, northwestern Queensland, are becoming well known for their preservation of the Miocene to Pleistocene record of mammalian evolution in Australia (Archer *et al.* 1989). Other vertebrate groups have also been recovered from these deposits; these include the lizards, a group which is numerically very important in the modern Australian fauna (over 500 species) but is all but unknown in the Australian fossil record. Covacevich *et al.* (1990) reported on the agamid lizards from Riversleigh, showing that this family was present at many of the fossil sites, with both modern and extinct taxa represented. This deals with the skinks (family Scincidae), the largest family of lizards and the largest family of terrestrial vertebrates in Australia (about 325 extant species in about 32 genera).

All Australian skinks belong to the subfamily Lygosominae, one of four scincid subfamilies defined by Greer (1970). In Australia there are three suprageneric groups, each apparently a monophyletic unit (Greer 1979, 1989): the *Sphenomorphus* Group (13 genera), the *Egernia* Group (3 genera) and the *Eugongylus* Group (16 genera). The *Egernia* Group is used here in the restricted sense of Greer (1979) rather than his later use of an expanded unit, the *Mabuya* Group (Greer 1989, Hutchinson 1981), as this latter unit may be paraphyletic.

This is a preliminary report on the scincid taxa identified to date at Riversleigh. Individual specimens will be described in detail and final taxonomic decisions made in future publications. Even at this preliminary stage of identification, it is apparent that the specimens recovered include some which strongly resemble modern taxa, some which are similar to, but can be differentiated from, modern taxa, and some which do not seem to have any close living relatives. On this basis, it is possible to summarise the composition of the Miocene skink fauna at Riversleigh and to arrive at some fairly firm conclusions regarding the origins and age of the Australian skink radiation.

Prefixes to specimen numbers are as follows: SAMA, South Australian Museum, Adelaide; UNSW AR, temporary University of New South Wales registration numbers for material collected by Dr Michael Archer and associates (all to be lodged eventually with the Queensland Museum).

DESCRIPTIONS

Lizard skulls, like those of most non-mammalian vertebrates, disarticulate *post-mortem,* so that specimens recovered from fossil deposits are most often isolated bones rather than partial crania or mandibles. This creates difficulties in identification since the literature on scincid osteology emphasises relationships between bones of intact skulls. The great majority of the fossil skink specimens recovered are lower jaw elements, mostly isolated dentaries, sometimes with one or more of the postdentary bones still in articulation. Characters of the scincid mandible which vary in taxonomically meaningful ways are indicated in Figure 1. The presence or absence of Meckel's groove, sutural relationships and degree of fusion of bones, positions of foramina and the shape of the retroarticular process have all been found to be useful in identifying skinks to varying degrees of precision.

Sphenomorphus Group

Most jaw fragments found have an open Meckel's groove, a primitive feature retained in the *Sphenomorphus* Group and in the subfamily Scincinae. Skinks of the latter taxon are not found in the modern Australian fauna, the closest occurrence of the group being the genus *Brachymeles* Duméril and Bibron from the Philippines (Greer 1970). Evidence for the Riversleigh specimens belonging to the *Sphenomorphus* Group comes from several nearly complete mandibles which preserve the articular region of the lower jaw. In these, the retroarticular process is almost parallel-sided, as is the case in living Australian members of the *Sphenomorphus* Group, with only a poorly developed, or no medially-directed expansion, as is the case in the Scincines examined by the author (the "inflected" condition described by Estes *et al.* 1988). Thus there is no reason as yet to think that the Scincinae has ever been present in Australia, and for now all dentaries with an open Meckel's groove are regarded as *Sphenomorphus* Group lygosomines.

"Sphenomorphus" spp. The genus *Sphenomorphus* Fitzinger is a grade group of generalised skinks at the base of the *Sphenomorphus* Group. In Australia, there are broadly two groups of species in this genus: a robust, long-legged and deep-bodied morphotype (treated by some recent workers as the genus *Eulamprus* Fitzinger: Cogger 1986; Greer 1989), and an attenuate morphotype with reduced limbs to which the same workers have applied the name *Glaphyromorphus* Wells and Wellington. Fossils attributable to both groups have been identified, representing very probably more than one species of each morphotype.

Two nearly complete mandibular rami (e.g. Fig. 2) represent a large member of the "robust *Sphenomorphus*" morphotype, and are structurally similar to the modern *S. murrayi* (Boulenger)

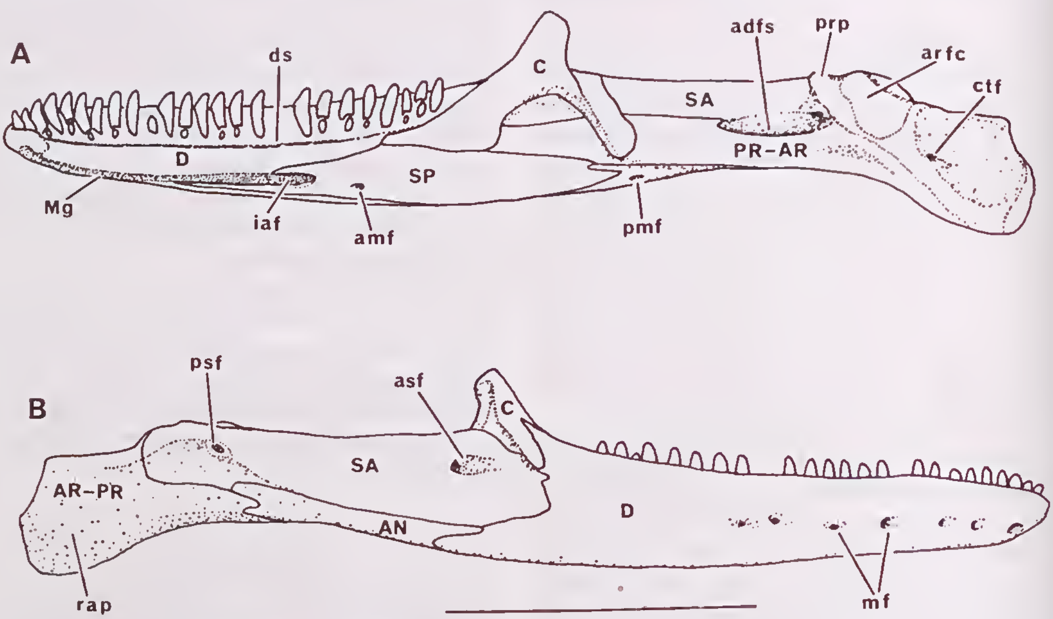

Fig. 1. Mandible of a primitive skink, the North American scincine *Eumeces fasciatus*, (SAMA R35701), in (**a**) lingual and (**b**) labial views. Scale bar equals 5 mm. Abbreviations: **adfs**, adductor fossa; **amf**, anterior mylohyoid foramen; **AN**, angular; **arfc**, articular facet; **AR-PR**, fused articular and prearticular; **asf**, anterior surangular foramen; **C**, coronoid; **ctf**, chorda tympanic foramen; **D**, dentary; **ds**, dental sulcus; **iaf**, inferior alveolar foramen; **mf**, mental foramina; **Mg**, groove for Meckel's cartilage; **pmf**, posterior mylohyoid foramen; **prp**, prearticular process; **psf**, posterior surangular foramen; **rap**, retroarticular process; **SA**, surangular; **SP**, splenial.

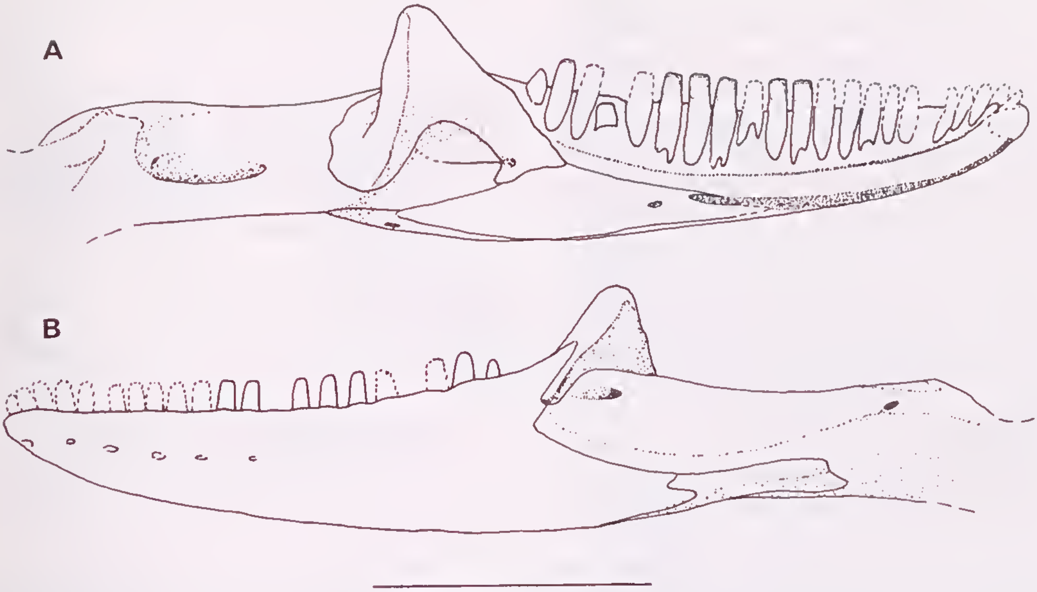

Fig. 2. Nearly complete left mandibular ramus of a robust member of the genus *Sphenomorphus (sens. lat.)*, (UNSW AR 17309, Camel Sputum Site), in (**a**) lingual and (**b**) labial views. Scale bar equals 5mm.

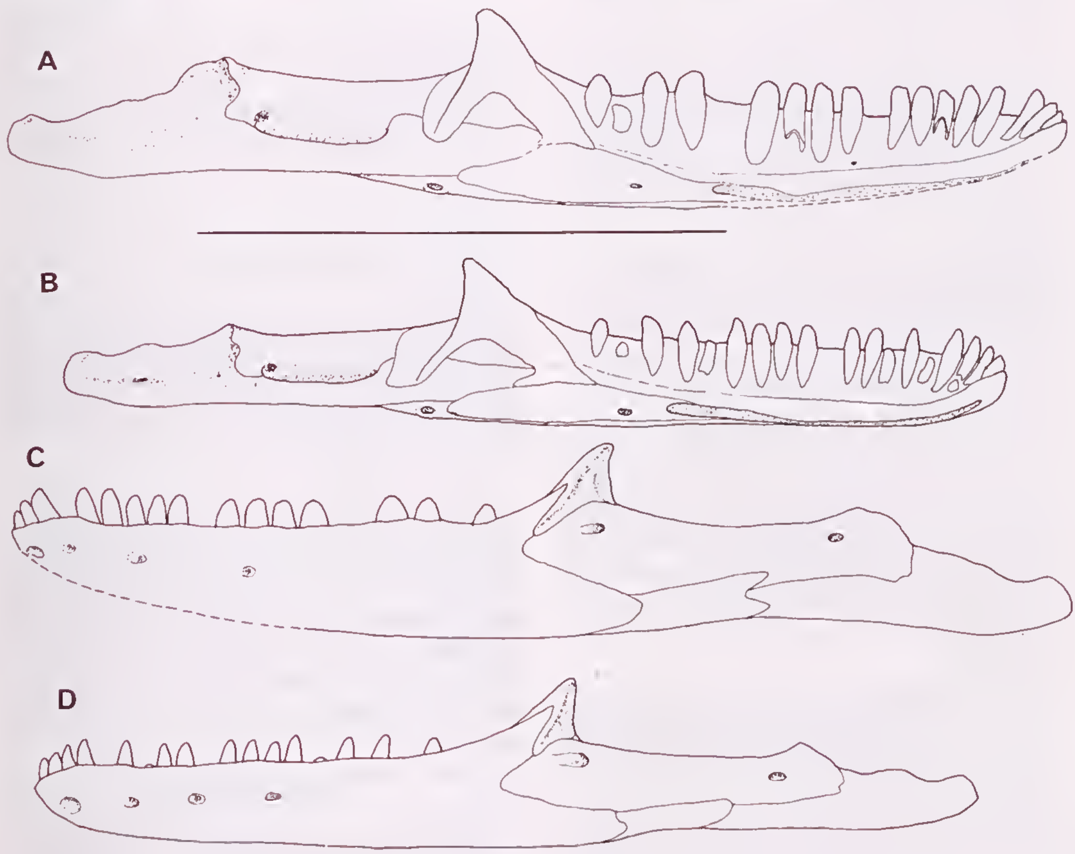

Fig. 3. Slightly restored left mandibular ramus of (**a** and **c**) an attenuate member of the genus *Sphenomorphus (sens. lat.)* (UNSW AR4550, Gag Site) compared with (**b** and **d**) a very similar living species, *Sphenomorphus mjobergi* (SAMA R35674). (**a**) and (**b**), lingual views; (**c**) and (**d**), labial views. Scale bar equals 5mm.

or *S. luteilateralis* Covacevich and McDonald. Small differences in the architecture of the coronoid and in the relative depth of the mandible suggest specific differentiation of the fossil. Other more fragmentary dentary remains may belong to a skink of this type, but might also belong to a water skink (*S. quoyii* complex). Isolated frontals, parietals and a quadrate are also attributable to this morphotypic group.

The "attenuate *Sphenomorphus*" morphotype is represented by a nearly complete mandibular ramus and is distinguishable from modern species such as *S. mjobergi* (Lönnberg and Anderson) or *S. punctulatus* (Peters) only by its slightly larger size and more robust teeth (Fig. 3). Additionally, isolated frontals have been found representing two taxa which have relatively broad interorbital regions and indications of narrow separation of pre-and postfrontals, and which might be attributable to skinks of this group (Fig. 4). In extant species, these modifications of the frontal are associated with fossorial habits and limb reductions.

Sphenomorphus Group, new genus and species. One of the best preserved skink finds is an almost complete mandibular ramus of a *Sphenomorphus* Group lizard not attributable to any living genus (Fig. 5). The teeth are relatively large and apparently durophagous. The mandible is relatively short and deep with high and deep insertions for adductor muscles. These proportions are not matched by any living species examined. The closest similarity is to *Lerista* Bell which may also have enlarged, durophagous teeth (Estes and Williams 1984), the larger species of which have a relatively short, bowed mandible with an unusually well-developed retroarticular process. However, the specimen lacks several derived features characteristic of *Lerista* and the similarities are probably analogous, suggesting similar modes of life rather than relationship. Several specimens referable to this taxon have been found at the Gag Site, including an isolated postdentary portion and other dentaries of possibly earlier ontogenetic stages.

Genus and species indeterminate - small insectivores. Numerous, but mostly fragmentary remains of quite small skinks (estimated skull length less than 12 mm) have an open Meckel's groove and tapering, pointed teeth such as those present in small insectivorous species of several genera (e.g. small *Ctenotus* Storr; Asian *S. sanctus* species-group). The fossils do not exactly match any extant member of the *Sphenomorphus* Group examined, and modern tropical Queensland skinks filling the insectivore niche are mainly members of the *Eugongylus* Group. The high frequency of dentaries of this morphotype suggests that one or more small skink taxa, now extinct, were an important part of the Riversleigh ecology.

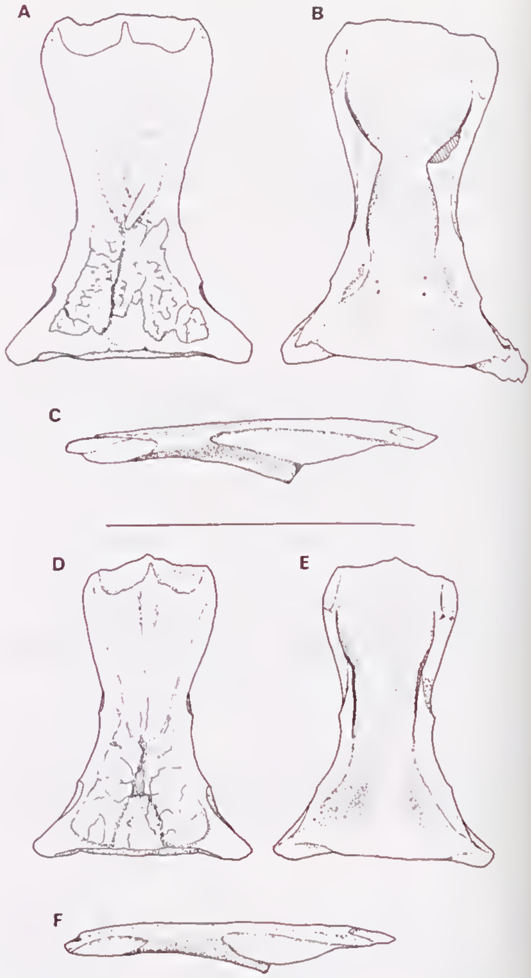

Fig. 4. Scincid frontal bones from the Gag Site (**a-c**, UNSW AR4419; **d-f**, UNSW AR 5340) in (**a, d**) dorsal, (**b,e**) ventral and (**c,f**) right lateral views. Both show a reduced gap between the prefrontal and postfrontal facets; UNSW AR4419 shows enhancement of the descending processes of the frontals. Scale bar equals 5mm.

Egernia Group

Several skink mandibles from Riversleigh have a closed Meckel's groove and a large, elongate inferior alveolar foramen positioned

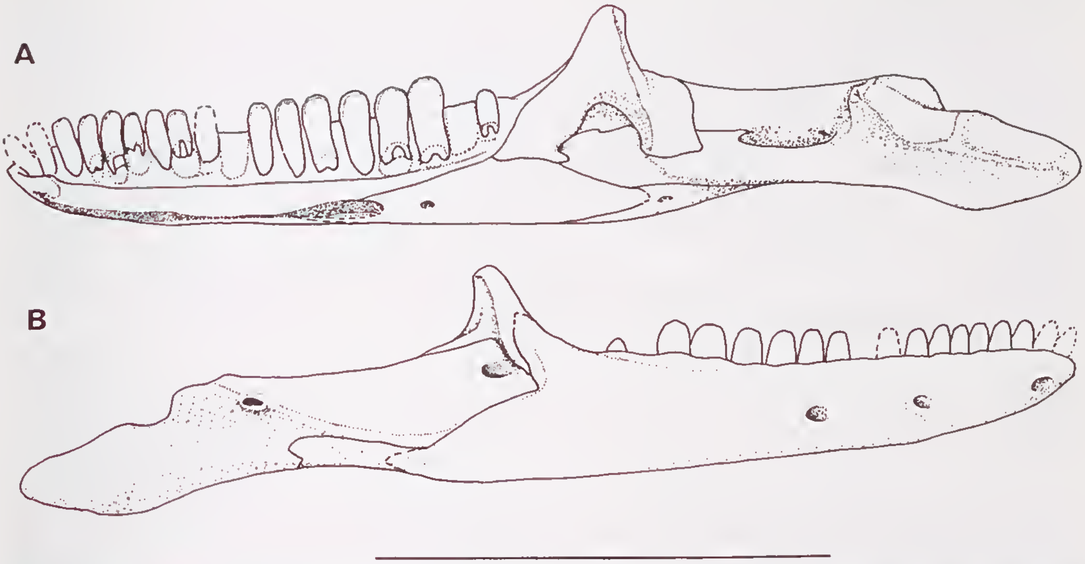

Fig. 5. Right mandibular ramus (restored; based mainly on UNSW AR5218, with details from UNSW AR4355 and UNSW AR4323, all Gag Site) of an undescribed member of the *Sphenomorphus* Group in (**a**) labial and (**b**) lingual views. Scale bar equals 5mm.

relatively low and anteriorly. This morphology is characteristic, in the modern Australian fauna, of the *Egernia* Group. Generic allocation in this group is based on tooth morphology; durophagous in *Tiliqua* Gray and *Cyclodomorphus* Fitzinger, slender in *Egernia* Gray.

Egernia frerei species-group. Tooth morphology does not vary much within the species groups defined by Horton (1972) and Storr (1978), but differs between them. Several fragments from Riversleigh have slender, chisel-crowned teeth which are identical to those found in large skinks of the *E. frerei* species-group (*E. frerei* Günther and *E. major* Gray: those of *E. rugosa* De Vis are similar, but not identical).

Egernia striolata species-group. A nearly complete anterior half of a mandible, plus several fragments, have teeth with crowns which are slightly labio-lingually compressed anteriorly, and expanded and rounded posteriorly. An identical morphology is seen in living members of the *Egernia striolata* species-group (Storr 1978), in which the differential pattern develops ontogenetically from a more homodont condition, in which all teeth are like the anterior teeth described above. The best preserved specimen is more robust than any living *E. striolata* Group jaws examined, but not extremely so (Fig. 6).

Tiliqua sp. nov. Shea and Hutchinson (1992) have identified two fragmentary dentary specimens from the Gag locality (System C, Middle

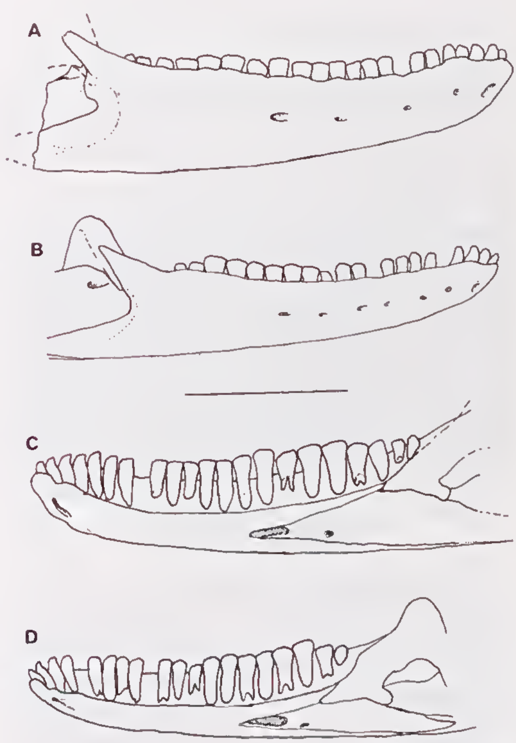

Fig. 6. Partly restored mandible of a species of (**a** and **c**) *Egernia* (UNSW AR 5212, Gag locality) compared with (**b** and **d**) a very similar living species, *Egernia striolata* (SAMA R24877). (**a**) and (**b**), labial views; (**c**) and (**d**), lingual views. Scale bar equals 5mm.

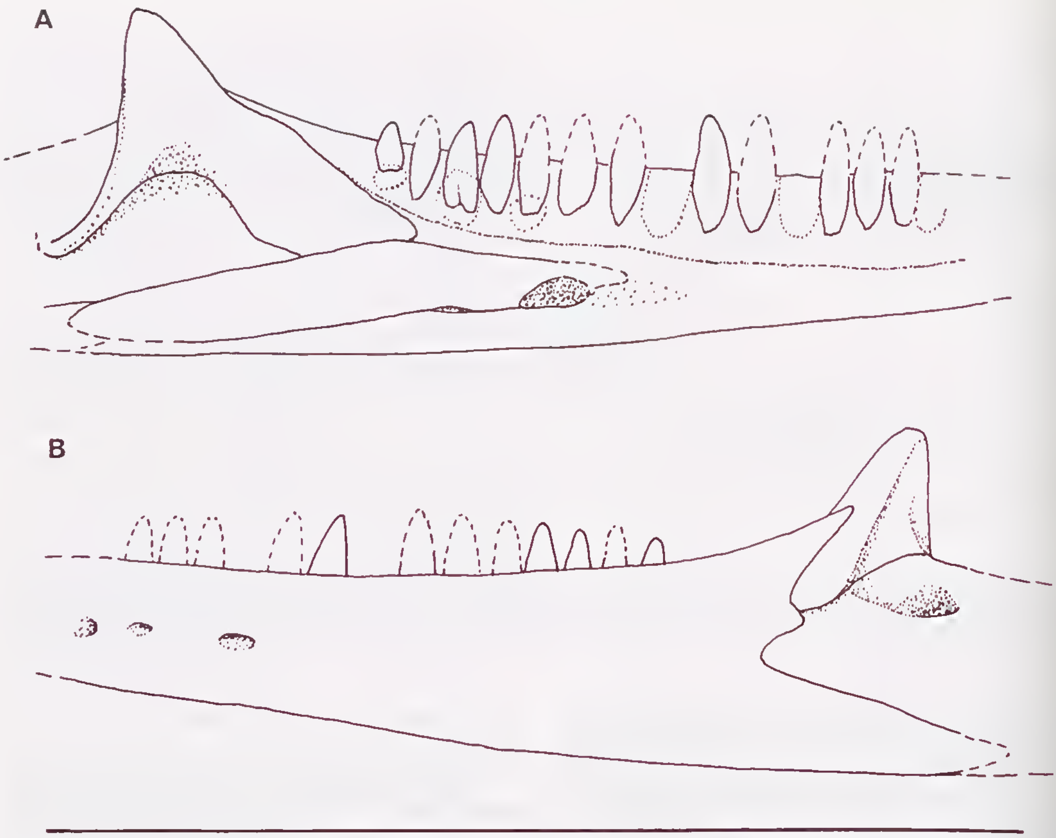

Fig. 7. Partial right mandible of a *Eugongylus* Group skink (UNSW AR17371, Ringtail Site) in (**a**) lingual and (**b**) labial views. Scale bar equals 5mm.

Miocene; Archer *et al.*, 1989) as a new species of this genus (in the restricted sense of Shea (1990)). It is much smaller than any living species of the genus, with the exception of *T. adelaidensis* (Peters), and although fragmentary, its distinctive teeth have allowed not only recognition of its generic relationship, but also permit its diagnosis as a new species. It is not obviously allied to any particular extant member of the genus.

Eugongylus Group

The rarest skink lineage at Riversleigh is the *Eugongylus* Group. Two well-preserved, informative specimens, plus several other fragmentary dentaries, have been recovered. Although rare, representatives of this lineage are stratigraphically widespread. A dentary and a partial mandible represent two different taxa, probably distinguishable at the generic level. The dentary is, in size and proportions, most like modern *Niveoscincus* Hutchinson *et al.* but differs in having more robust, pointed teeth, compared with the blunt-crowned teeth of *Niveoscincus.* The partial mandible is most like modern *Carlia* Gray in the shape of the coronoid and the dentary-surangular contact, and in having a dorsally-oriented opening for the anterior surangular foramen. However, in proportions the jaw appears to be shorter than in modern *Carlia.* This estimation is based on the position of the inferior alveolar foramen (Fig. 7) which is separated from the most posterior mental foramen by a distance equal to eight to eleven tooth loci in *Carlia,* but only five tooth loci in the fossil.

COMPARISON OF MODERN AND MIOCENE FAUNAS AND THE ORIGINS OF THE AUSTRALIAN SKINKS

The stratigraphic distribution of provisionally identified skink taxa is summarised in Table 1. This is likely to give an underestimate of the true diversity, since several species or even genera

TABLE 1. Distribution of fossil skink taxa at Riversleigh sites; + = present. 1, robust *Sphenomorphus* (more than one taxon); 2, attenuate *Sphenomorphus* (more than one taxon); 3, durophagous taxon ("erusher"); 4, small inseetivore; 5, *Egernia* ef. *frerei*; 6, *Egernia* cf. *striolata*; 7, *Tiliqua* sp. nov.; 8, indeterminate genus (more than one taxon).

Site	*Sphenomorphus* Group				*Egernia* Group			*Eugongylus* Group
	1	2	3	4	5	6	7	8
Early to mid Miocene								
"System C"								
Henk's Hollow	+	+		+				
Two Trees	+		+	+				+
Ringtail		+		+				+
Wang		+						
Gag	+	+	+	+	+	+	+	
Early Miocene								
"System B"								
Neville's Garden	+	+	+	+	+			+
Boid Site East	+					+		+
Camel Sputum	+	+	+	+	+			+
Helicopter		+	+		+			
Inabeyance								+
Mike's Menagerie	+	+		+				
Upper		+	+	+	+	+		+
VDU	+							
Outasite		+						
RSO		+						
Wayne's Wok		+		+		+		
Wayne's Wok 2		+		+				

may well be lumped in some of the column categories. Table 2 compares the early to mid Miocene Riversleigh skink fauna to the modern faunas of southeastern and northeastern Queensland forests.

The faunas are similar in being dominated by the *Sphenomorphus* Group, with the *Egernia* Group present, but, as a minor faunal component. They differ in apparent generic composition, with seemingly fewer specialised taxa being present during the Miocene. The *Eugongylus* Group appears to be relatively rare at Riversleigh, compared to its moderate frequency in modern Queensland forests. Living members of this group are predominantly small, but their rarity at Riversleigh cannot be simply attributed to physical taphonomic factors. The relative abundance of *Sphenomorphus* Group remains, which are just as small, indicates that hydrodynamic sorting, for example, has not influenced the frequency of occurrence of the *Eugongylus* Group in this deposit. It is possible that the Riversleigh Miocene ecosystem was depauperate in *Eugongylus* Group skinks, and that their role as small insectivores was filled by small members of the *Sphenomorphus* Group.

Prior to the acceptance of continental drift, and to the modern studies of scincid phylogeny, the family was viewed as a relatively recent arrival in Australia, with a relatively low level of endemicity at the genus level (Keast 1959; Storr 1964). Subsequent to this, it has become clear that skinks show a higher degree of generic endemism than previously thought (e.g. *Leiolopisma*, Hutchinson *et al.* 1990). Discovery of the oldest "skinks" on a Laurasian landmass implied a northern origin (Cracraft 1974; Estes 1983b), and the wide gap thought to have separated Australia and Southeast Asia during the Palaeogene (Smith and Bryden 1977) seemed consistent with a recent arrival of the family in Australia (no earlier than Miocene). Recent advances in the understanding skink phylogeny identify centres of endemism in Australia, tropical Asia and Africa-Madagascar, suggesting a Gondwanan, rather than Laurasian, origin for skinks.

Fossil data on the past distribution of skink lineages would clearly contribute greatly to resolving both the geography and timing of their origins. In spite of its size and global distribution, the family Scincidae has a very poor fossil record both in Australia and elsewhere (Estes 1983a, 1983b). Indisputable skinks first appear in the Oligocene of North America, with specimens allocated to the still living (although archaic) *Eumeces* Wiegman. North American scincoid remains from the Eocene, Paleoeene

TABLE 2. Comparison of the Riversleigh skink fauna with skink faunas of modern northeastern, and southeastern Queensland " + " denotes the presence of a taxon, " - " its absence.

Genus	Northeastern Queensland	Southeastern Queensland	Riversleigh
***Sphenomorphus* Group**			
Anomalopus	+	-	-
A. reticulatus sp. group	+	+	-
Calyptotis	+	+	-
Ophioscincus	-	+	-
Saiphos	-	+	-
robust *Sphenomorphus*	+	+	+
slender *Sphenomorphus*	+	-	+
"Tropidophorus"	+	-	-
Riversleigh "insectivore"	?	?	+
Riversleigh "crusher"	-	-	+
***Egernia* Group**			
Cyclodomorphus	+	+	-
Egernia	+	+	+
Tiliqua	-	-	+
***Eugongylus* Group**			
Carlia	+	+	-
Lampropholis	+	+	-
Lygisaurus	+	+	-
Genus indet.	?	?	+
TOTAL	11	10	7

and Late Cretaceous are too incomplete to be identified with confidence as skinks. There is a wider geographic representation from the Miocene onwards, with records from several North American sites, Morocco and Australia, but diversity is still very low. Just two genera are recorded from the Miocene: *Eumeces* in America and North Africa and *Egernia* in Australia (Estes 1984). Only in Plio-Pleistocene sediments do skinks become relatively diverse, but these faunas are not significantly different from living skinks in the same geographic areas.

The Riversleigh Tertiary skink fauna is the richest yet recorded and the first from a land mass rich in living skinks. These finds show that the mid-Tertiary skink fauna was already completely Australian in character. Not only were all three lygosomine generic groups present, but they were also diverse, and both extant and extinct genera seem to have been present. These fossils support the idea that the modern Australian skink fauna is largely the product of *in situ* evolutionary radiation, rather than waves of invaders which differentiated elsewhere. The presence of the three lygosomine groups in the Riversleigh Miocene indicates that their origins must predate the Oligo-Miocene boundary. The suggestion of an earliest Tertiary date for their phylogenetic divergence, based on immunological data on albumin evolution (Baverstock and Donnellan 1990), is compatible with the estimated age of the Riversleigh fossil fauna.

The ultimate origin of Australia's skinks is not clarified by these finds. Recent reviews of data on continental drift (Audley-Charles 1987; 1991) concluded that Australia's isolation from Asia during the Tertiary was less complete than previously believed and also that it separated from Antarctica earlier than previously thought; i.e. prior to the Eocene. If lygosomines evolved outside Australia and first arrived around the K-T boundary, they had to cross via an archipelagic sweepstakes route, whether they came via the Indo-Malayan archipelago or East Antarctica. As Greer (1979) suggested, the number of "sweepstakes winners" necessary to establish the Australian fauna was probably no more than one to three.

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